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**Long-term Effects of Multiple Disturbances on Soil Properties and Regeneration in a
Colorado Subalpine Forest**

By:
Kelsey Kay Bickham
Ecology and Evolutionary Biology, University of Colorado at Boulder

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Thesis Advisor:
Dr. Carol Wessman, CIRES/Ecology and Evolutionary Biology

Defense Committee:
Dr. Carol Wessman, CIRES/Ecology and Evolutionary Biology
Dr. Barbara Demmig-Adams, Ecology and Evolutionary Biology
Dr. Thomas Veblen, Geography

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Kelsey Kay Bickham

Abstract

Compound disturbances occur when multiple disturbances happen in rapid succession, and may result in changes to ecosystem recovery processes. Activities performed by management agencies, such as salvage-logging, following severe disturbances may act as a compound disturbance by altering the ecosystem's recovery mechanisms. The site of the present study, located in Routt National Forest, Colorado, sustained a catastrophic blowdown event that impacted over 10,000 ha in 1997 and was partially salvage - logged between 1998 and 2001. The present study evaluates the interacting effects of these two disturbance events on soil characteristics, seedling regeneration, growth and density, and any changes to community composition. These measurements were recorded within ten heavily wind-damaged *Picea-Abies* stands, ten salvage - logged blowdown stands, and ten intact control stands. While soil characteristic results suggest a long-term significant difference between treatments, trends initially observed post disturbance generally diminished over time. Similarly, regeneration characteristics were significantly different between treatments but less significant so than for the short-term effects. This apparent differential recovery suggests that salvage-logging following severe blowdown results in reduced regeneration and in lasting alterations of soil properties. The present findings thus suggest that salvage-logging does act as a compound disturbance. With climate change, more frequent and severe disturbances may occur, and it is thus necessary for management agencies to quantitatively evaluate the potential compounding effects of their decisions.

Introduction:

Disturbances are important, but not well understood processes that disrupt ecosystem, population or community structure and change resource availability (Pickett and White 1985). Disturbances such as wind, fire and insects are critical drivers in the structuring of subalpine forest landscapes (White and Pickett 1985). However, the occurrence of multiple disturbances in rapid sequence may affect typical successional processes (or ecosystem recovery) in unusual ways. What are the long-term effects of multiple disturbances and their interactions on species composition and forest structure in subalpine ecosystems? The present project evaluates multiple disturbance effects on soil properties and regeneration of a subalpine forest 15 years after a catastrophic wind-storm (or blowdown) and subsequent salvage-logging in northern Colorado. Specifically, I address the following hypotheses:

H₁: Differences in soil properties initially observed between areas subject to blowdown, salvage-logged blowdown, and green, intact forest areas will remain 15 years after the events because of the initial severity of the disturbances.

H₁₁: Total soil carbon and nitrogen levels will be lower in logged areas than in blowdown and control areas.

H₁₂: High soil compaction (bulk density) observed in logged blowdown will remain 15 years after the event.

H₂: Regeneration will remain significantly altered in logged areas compared with blowdown areas 15 years after the disturbances because establishment of new individuals is hampered by inhospitable soil conditions, and the increase in understory graminoid cover.

H₂₂: Seedling densities will be lowest in logged blowdown treatments.

H₂₃: Species composition in logged blowdown sites will shift toward lodgepole dominate.

In 1997, a severe windstorm blew down more than 10,000ha of forest (also referred to as blowdown) in the Routt National Forest of northern Colorado, the largest recorded blowdown in southern Rocky Mountain history (Baker et al. 2002). The impact of the blowdown was concentrated in subalpine forest (Kulakowski and Veblen 2002, Rumbaitis-del Rio 2006). Salvage-logging operations using tractors, helicopters, and cable logging systems were conducted from 1998 to 2001 in some severely blown down areas, in which typically over 80% of the trees were blown down (Rumbaitis-del Rio 2006). A previous study conducted by Rumbaitis-del Rio and others (2006) examined this ecosystem and measured the immediate effects of these disturbances. The objective of the present study is to examine soil properties and regeneration patterns 10-15 years following the disturbances, and to compare current conditions to those measured in the initial years post-disturbance. This comparison with the previous study will allow for quantitative evaluation of the ecosystem's response and regeneration following these disturbances.

Very few quantitative studies have evaluated catastrophic wind disturbance events in coniferous forest or the consequences of salvage-logging following blowdown. This study will provide insight into how subalpine ecosystems react, recover, and regrow following wind disturbance and subsequent salvage-logging. This study will be one of few to compare very early observations of regeneration and soil responses to multiple catastrophic disturbances with the state of the system after more than a decade of recovery.

Background

Forest ecosystems are complex, adaptive and dynamic with many variables contributing to the fundamental identity, structure and function of this ecosystem (Pickett and White 1985). An integral part to the functioning of all ecosystems is disturbance (Attiwill 1994) defined as any

relatively discrete event that disrupts ecosystem, population or community structures, and alters substrate or resource availability (Turner 1989). Ecosystems can experience many types of disturbance events that are abiotic, biotic, or climatic. Disturbances are therefore classified by frequency and magnitude of the event (White and Pickett 1985). The ecosystem's recovery or succession is dependent on the historical range of variability for that system (Turner 2010). The historical range of variability for a forest ecosystem is the adaptive range of the system, or simply, what the system is capable of withstanding over one or many generations (Veblen 2003). The capacity of a forest to withstand a variety of disturbances and maintain its fundamental identity, structure and function is the resilience of that system (Folke et al. 2004, Seidl et al. 2011). Resilience is not limited to the system's ability to recover, but also its ability to reorganize or adapt. The capacity of an ecosystem to reorganize to its original functional and structural identity or to adapt to new conditions is directly proportional to the disturbance or disturbances that caused the change (Veblen 2003). Consequently, disturbance is key to ecosystem functioning and productivity (Everham and Brokaw 1996, Kulakowski et al. 2003).

Disturbances can affect multiple aspects of a forest ecosystem, such as processes involved in nutrient cycling (Attiwill 1994), measures of biodiversity (Turner 1989), and susceptibility to future disturbances (Veblen et al. 1994). Although most disturbances are considered to be large, infrequent and singular events (Attiwill 1994), it should be noted that one disturbance is can be followed by one or more additional events. A combination of disturbance events is referred to as a compound disturbance (Rumbaitis-del Rio 2006), in which successional pathways following an initial event are interrupted by another disturbance.

Considerations of disturbance regimes, that include natural disturbances such as fire, herbivory and climatic changes (Veblen et al. 1994), often neglect to include more catastrophic

disturbance events (Rumbaitis-del Rio 2006). A catastrophic disturbance that is particularly poorly understood is wind disturbance, such as tornadoes, hurricanes, microbursts, wind storms and gales (Everham and Brokaw 1996, Cooper-Ellis et al. 1999). Yet, these disturbances affect nearly every forest around the globe and can significantly alter forest composition, succession and regeneration (Rumbaitis-del Rio 2006). The importance of wind disturbance events has primarily been studied in temperate deciduous forests of the northeastern United States, and therefore cannot necessarily be generalized to reflect the full effects on coniferous forests (Veblen et al. 1989, 1991, Rumbaitis-del Rio 2006). However, certain aspects of wind disturbance are general to multiple forest types. For example, that windthrow events (or blow downs) may alter stand structure, succession and productivity of forest ecosystems (Everham and Brokaw 1996, Peterson 2000). Blowdown damage severity and pattern may be partially determined by the prestorm forest composition or structure, which may leave biological legacies, and which may in turn alter ecosystem recovery processes (Veblen et al. 2001). The ecosystem recovery process has been observed to be related to the severity of the blowdown event (Kulakowski and Veblen 2003).

Nearly all forms of wind disturbance decrease stand structure by damaging or downing susceptible trees (often the larger trees) and thus increase woody debris on the forest floor (Everham and Brokaw 1996, Tinker and Knight 2000). This increase in woody debris can intensify the probability of a compound disturbance such as wild fire or insect outbreak (Kulakowski and Veblen 2002). The forest's productivity is altered following a blowdown that removes the canopy and exposes the understory species, allowing an increased potential for vegetative growth (Attiwill 1994). The loss of trees reduces regeneration from seed in coniferous

species (Veblen et al. 1991), and advanced conifer regeneration in the understory becomes the primary mechanism of regeneration (Rumbaitis-del Rio 2004).

In subalpine forests, the loss of coniferous species promotes growth of deciduous species, such as aspen, whose growth was restricted before disturbance (Baker et al. 2002, Greene et al. 2006). This is generally considered to be a common successional process within subalpine ecosystem dynamics (Long 2003). Succession is the process of recovery from disturbance within an ecosystem; for example, within subalpine ecosystems it is common for species like aspen to proliferate following disturbance, and as time passes coniferous species reestablish to approximate predisturbance community composition (Allen and Holling 2010). However, if coniferous species do not reestablish and aspen remain as the dominant species, a shift in ecosystem type can occur (D'Amato et al. 2008), which is also referred to as a species regime shift (Folke et al. 2004). This change in community composition is of concern because the functionality of the ecosystem may be altered, with unknown consequences for the larger-scale landscape (Frolking et al. 2009, Buma and Wessman 2012). However, the importance of such events varies for differing ecosystems, and may be a function of the ecosystem's resource availability, disturbance regime, historical range of variability, and resilience (Veblen et al. 1991, Busby et al. 2009).

Following catastrophic disturbance, land management agencies such as the United States Forest Service (USFS) often perform salvage-logging (Rumbaitis-del Rio 2006). Salvage-logging is a practice where, following events that damage or blow down trees, logging occurs to remove potentially profitable timber and/or reduce fuel loads and decrease the risk of subsequent disturbances (Schwilk et al. 2009). The effect of salvage-logging on ecosystems is a controversial issue (Dellasala et al. 2006). The USFS maintains that salvage-logging poses no

additional effects on an already disturbed ecosystem (Rumbaitis-del Rio 2006). However, Beschta (1995) claim that management practices, including salvage-logging following fire disturbance, causes drastic negative effects on ecosystem recovery. There have been few quantitative studies on the effects of salvage-logging (Lindenmayer 2006) and even fewer assessing salvage-logging after wind disturbances and its effect on forest structure, composition, and recovery (Foster and Orwig 2006). However, the use of heavy machinery involved in logging practices (such as tractors), is thought to cause increased soil compaction, increases erosion, and reduces soil organic matter (Beschta 1995, Noss and Lindenmayer 2006), effects are likely to alter an ecosystem's ability to recover (Foster and Orwig 2006, Saint-Germain and Greene 2009).

Consequently, more research is needed on the effects of wind disturbance in coniferous forests, as well as possible compounding effects of subsequent salvage-logging on these ecosystems. The wind disturbance followed by salvage-logging in Colorado's Routt National Forest presents an excellent opportunity to examine these disturbances and their interactions. The present study aims to evaluate the effects of catastrophic wind disturbance followed by subsequent salvage-logging on conifer regeneration and edaphic (soil) characteristics more than 10 years post-disturbance. The present study is important to understand the longer-term responses of a subalpine coniferous forest to compound wind and salvage-logging disturbances.

Methods

Study Site:

The study site was Routt National Forest in northwestern Colorado, USA (40°47'N, 106°15'W) (Rumbaitis-del Rio 2006). Elevation ranges from 2500 to 3300 m above sea level. The dominant canopy species within the study area are subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and quaking aspen

(*Populus tremuloides*). Soils originated from Precambrian granites, gneiss and glacial deposits (Rumbaitis-del Rio 2006), and are classified as typic Cryochrepts and Dystrocryepts (Rumbaitis-del Rio 2006). The climate is considered continental with mean annual temperature of 3.83°C, ranging from -8.3°C in winter, and 15.1°C in the summer months (WRCC, 2012). Mean annual precipitation is 60.88 cm (Western Regional Climate Center, 2012). Precipitation in this area is high compared to surrounding areas, and generally comes from high amounts of winter snowfall and summer monsoons (Rumbaitis-del Rio 2006).

This mature subalpine forest was subject to a substantial wind storm, affecting approximately 10,000 ha on October 25, 1997 (Rumbaitis-del Rio 2006). Wind speeds exceeding 200 km / hr, associated with an early season blizzard resulted in the largest recorded blowdown in the Southern Rocky Mountain region (Rumbaitis-del Rio 2006). The blowdown created approximately 400 patches of downed trees, with sizes ranging from <1 to ~310ha (Baker et al. 2002). Because of the increased risk for an epidemic beetle outbreak (Kulakowski and Veblen 2003), the USFS conducted tractor-, cable-, and helicopter- based salvage-logging from 1998-2001 on 935 ha of blowdown patches (Rumbaitis-del Rio 2006).

In May of 2000, Rumbaitis-del Rio (2006) had established 15 plots (400 m² each) in the study area. Five plots in unlogged patches of high-severity blowdown, five plots in blowdown patches that had been salvage - logged with tractors in 1999, and five control plots in intact, green forest. Blowdown and salvage - logged plots were located in large patches of heavy blowdown damage. Minimizing the effects of predisturbance vegetation differences, all plots were located in stands constituted primarily of Engelmann spruce and subalpine fir, with no aspens in the plots.

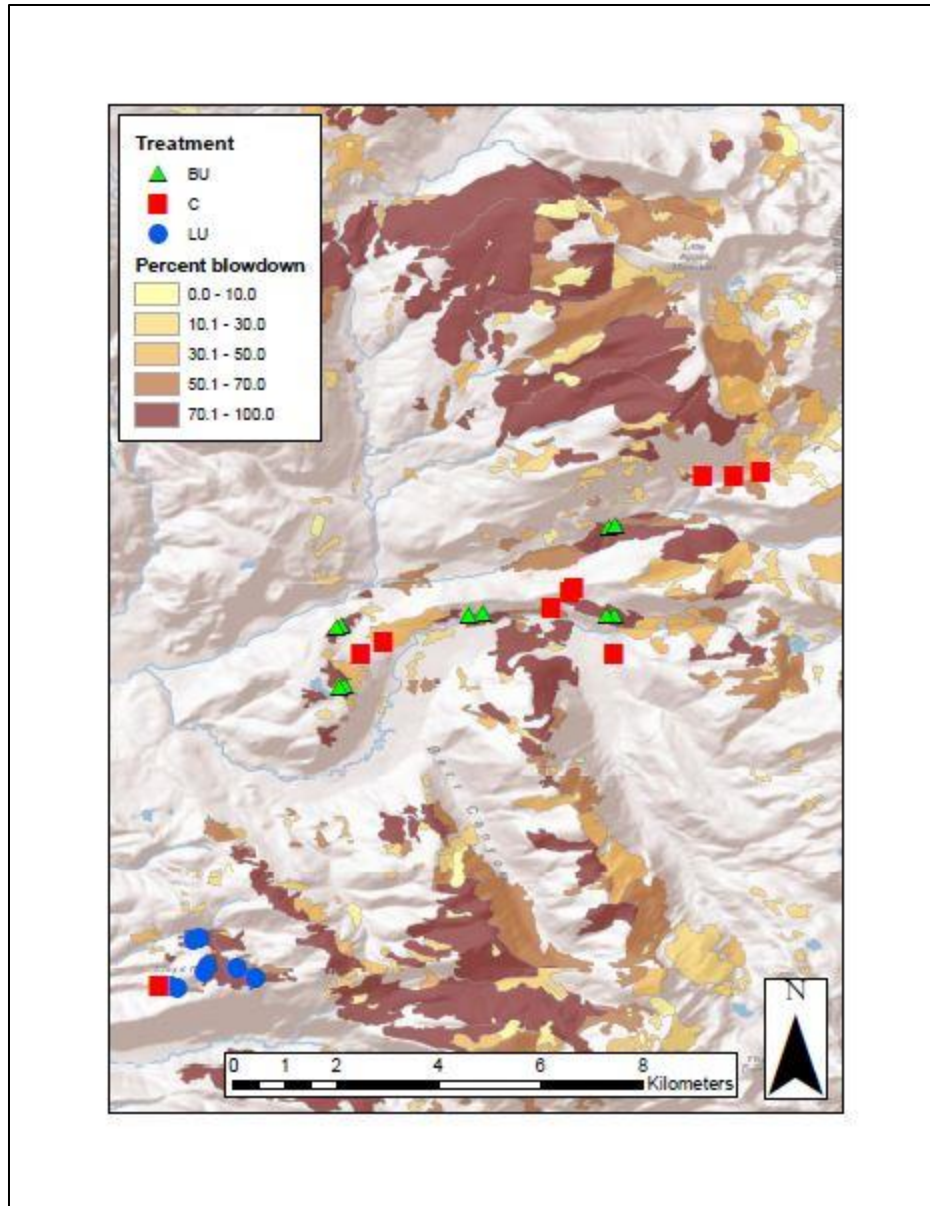


Figure 1: Map of the study site location, showing topography and the percentage of blowdown per blowdown patch and location of all plots. (Veblen et al.)

Field Measurements:

During summer 2012, 10 (15 X 15 m) plots for each of three treatment types ($N_{\text{Total}} = 30$) were located via GPS in areas of the Routt National Forest of green, intact forest (control sites) or which had experienced blowdown (BU), or blowdown and salvage-logging (LBU). Several measurements of vegetation and soil properties were made in each plot. Ten 10 cm deep soil

cores were taken from randomly selected points within each plot for every treatment. Soil cores were separated into organic and mineral horizons in the field, and depth of soil horizons were directly measured with a metric tape and recorded. Seedlings and trees were counted, with seedlings considered to be any tree less than 150 cm tall. Height was measured for all trees using an inclinometer, and seedlings were measured with a meter tape. Diameter at breast height (DBH) was taken for all trees with heights greater than 150cm. Fractional cover was measured in 10 randomly placed 1m² areas to determine major functional groups, including grasses, forbs (or herbaceous flowering plants other than grasses), bare soil, rocks, seedlings, and woody debris. Coarse-woody debris was recorded following Van Wagner's (1968) line-intersect method along the two 21.2m diagonals of each plot to quantify the amount of fuel on the ground from the number and size of debris crossing the transect. The decay class of the coarse woody debris was also measured in accordance with USFS methods, with sound (not rotten) wood being decay class 1-2, and rotten wood being decay class 3-5.

Laboratory Analysis:

Soil samples taken in the field were weighed and then dried in a 60°C oven for 24 hours. Soils then were sieved through a 2-mm mesh sieve to separate each organic and mineral core into coarse and fine particles. Once separated, five of the 10 organic samples from each plot that had been weighed, dried and sieved were re-dried at 105°C for 24 hours to remove all remaining moisture, then weighed again to calculate soil moisture. Soil moisture was calculated by subtracting the weight of the pre-dried samples from the weight of the samples after they had been dried (at 105°C), giving grams of water as a fraction of the total weight. Bulk density was calculated for the organic, mineral and top 10cm soil horizons in accordance with Throop et. al. (2012). This was done by determining the ratio between the post-dry weights to the volume of

the respective soil horizon, giving a measure of soil compaction. Organic horizon mass was calculated by weighting the bulk density of the organic horizon by its depth. Subsamples were taken from soil cores which were only dried at 60°C and ground for the time necessary to create a homogeneous mixture (particles capable of passing through a 250 µm mesh) for combustion analysis. Chemical analyses of the subsamples were performed using an Eager 1108 CHN elemental analyzer in order to find the percentage of carbon and nitrogen concentrations, and the ratio of carbon to nitrogen for each plot. Seedling counts were converted to seedling density by dividing the number of species per plot by the area of the plot in square meters.

Statistical Analysis

Plot level metrics were averaged to provide consistent sample numbers for the use in statistical testing. Statistical analysis was performed using the statistical program R (Team 2012). Analysis of covariance (ANCOVA), a form of general linear regression and analysis of variance (ANOVA), uses covariance as a measure of how two variables change together and the strength of the relationship between them. ANCOVA evaluates whether the means of the dependent variable are equal across levels of the independent variable, while statistically controlling the effects of continuous variables not of interest (referred to as covariates). ANCOVA was chosen as the preferred statistical test because it adjusts the dependent variables means to remove the unwanted effects of the independent variables not of interest. The dependent variables were the outcome variables of interest (i.e. soil moisture, seedling density, bulk density, depth of organic horizon, etc.). The categorical independent variable was treatment (control, blowdown, and logged), and the continuous independent variables not of interest were elevation, slope and aspect. ANCOVA increases the probability of finding a significant treatment effect by reducing

the amount of within-group variance caused by the effects of the unwanted independent variables.

The ANCOVA process constituted: 1) a linear model which evaluated linear relationships between dependent and independent variables, 2) an ANOVA performed on the outcome of the linear model to remove covariates, and 3) a post-hoc analysis (Tukey's Honestly Significant Difference test, HSD) on the results of the ANOVA to determine any significant treatment differences. Tukey's HSD was the preferred post-hoc test because of its relative strength compared to a more conservative Bonferroni correction test. All statistical tests were performed using the alpha level (confidence interval) of $\alpha < 0.05$. Results are written in the order of the ANCOVA procedure, with the results of the linear model first, followed with significant effects from the ANOVA and finally any significant treatment effects from Tukey's HSD. If not referred to specifically, the covariates elevation, slope and aspect are also referred to as the variables of topography.

Results

Soil Properties

Soil horizon depths were not significantly different between treatments (Fig. 2). The depth of the organic horizon was found not to be significantly different between treatments after controlling for the effects of elevation, slope, aspect and the interactions between treatment and elevation, slope or aspect ($F(11,18) = 0.97, p = 0.5$). The depth of duff after similarly controlling for elevation, slope and aspect showed significance ($F(11, 18) = 2.37, p = 0.05$), caused by a significant treatment effect ($F(2) = 6.096, p = 0.009$), which was determined to be caused by a significant difference between control and blowdown ($p = 0.009$).

The soil moisture of the organic horizon was not significantly affected by elevation, slope or aspect ($F(11,18)= 1.314$, $p= 0.29$), but did show a significant treatment effect ($F(2)= 4.471$, $p= 0.026$), which was determined to be caused by a nearly significant difference between logged and control treatments ($p= 0.06$, Fig. 2). The soil moisture of the mineral horizon showed marginal significance ($F(11,18)= 2.357$, $p= 0.052$), caused by a significant effect from elevation ($F(1)= 8.055$, $p= 0.01$), and treatment ($F(11,18)= 3.837$, $p= 0.04$). After controlling for the effects of topography, there were no significant differences between treatments. The soil moisture of the top 10cm of soil was found not to be significantly affected by elevation, slope, aspect or their interactions with treatment ($F(11,18)= 2.31$, $p= 0.06$), but did show a significant treatment effect ($F(2)= 7.054$, $p= 0.005$), which was determined to be caused by a significant difference between control and blowdown treatments ($p= 0.013$), and between logged and control treatments ($p= 0.03$).

Bulk density of the organic horizon did not show significant differences between treatments after similarly controlling for topographic variables ($F(11,18)= 1.562$, $p= 0.2$), caused by a significant effect from slope ($F(1)= 5.335$, $p= 0.03$). A highly significant effect of elevation ($F(1)= 15.623$, $p= 0.0009$) led to no significant differences between treatments for the bulk density of the mineral horizon ($F(11,18)= 2.109$, $p= 0.08$). Bulk density of the top 10cm of soil after controlling for the same topographic variables also showed no significant differences between treatments ($F(11,18)= 1.677$, $p= 0.16$), caused by a significant effect from elevation ($F(1)= 11.763$, $p= 0.003$). Organic horizon mass per hectare similarly showed no significant treatment differences after controlling for the same topographical variables ($F(11,18)= 1.484$, $p= 0.2$).

The amount of carbon (Mg/ha) for the mineral horizon, after controlling for the effects of topography, showed significant treatment differences ($F(11,18)=4.005$, $p= 0.005$), from a significant treatment effect ($F(2)= 13.373$, $p= 0.0003$), and significant interaction between aspect and control ($F(2)= 4.822$, $p= 0.02$); the significant treatment effect was a result of significant differences between control and blowdown ($p= 0.0003$) and logged and control ($p= 0.013$). The amount of nitrogen (Mg/ha) of the mineral horizon, after controlling for the same effects, also showed significant treatment differences ($F(11,18)= 2.562$, $p= 0.04$), with a significant treatment effect ($F(2)= 6.728$, $p= 0.006$), caused by a significant difference between control and blowdown ($p= 0.007$) and between logged and control ($p= 0.06$). However, the carbon to nitrogen ratio (C:N) for the mineral horizon showed significant treatment differences ($F(11,18)= 2.915$, $p= 0.021$) as a result of highly significant effects from slope ($F(1)= 20.576$, $p= 0.0002$). Differing from the mineral horizon, the amount of carbon (Mg/ha) of the organic horizon did not show significant treatment differences ($F(11,18)= 1.689$, $p= 0.2$), caused by a significant effect from slope ($F(1)= 4.681$, $p= 0.04$), and aspect ($F(1)= 5.86$, $p= 0.03$). The amount of nitrogen (Mg/ha) of the mineral horizon after controlling for topography also showed no significant treatment differences ($F(11,18)= 1.578$, $p= 0.2$), with a significant effect from slope ($F(1)= 4.615$, $p= 0.04$). The carbon and nitrogen ratio for the mineral horizon also showed no significant treatment differences after controlling for topography ($F(11,18)= 1.246$, $p= 0.3$).

Table 1:

A summary of mean soil characteristics of interest compared against treatments (\pm S.D.) N=30, 10 plots per treatment.

Treatment	Control	Blowdown	Logged
Duff Depth (cm)	2.3 \pm 0.9 ^a	1.3 \pm 0.7 ^b	1.4 \pm 0.6 ^c
Organic Depth (cm)	4.8 \pm 2.0	3.5 \pm 1.6	2.8 \pm 2.5
Organic Depth (cm) [*]	4.15 \pm 0.44	6.12 \pm 0.86	1.48 \pm 0.42
Soil Moisture Top 10cm (g H ₂ O / g dry soil)	0.36 \pm 0.15 ^a	0.20 \pm 0.07 ^b	0.15 \pm 0.07 ^{bc}
Soil Moisture (g H ₂ O / g dry soil) ¹	0.29 \pm 0.0333	0.29 \pm 0.0333	0.24 \pm 0.027
Bulk Density Organic (g/cm ³)	0.17 \pm 0.04	0.23 \pm 0.09	0.20 \pm 0.09
Bulk Density Mineral (g/ cm ³)	0.51 \pm 0.11	0.41 \pm 0.12	0.62 \pm 0.13
Top 10 cm Bulk Density (g/ cm ³)	0.39 \pm 0.09	0.36 \pm 0.10	0.55 \pm 0.13
Top 10 cm Bulk Density (g/cm ³) [*]	0.79 \pm 0.04	0.81 \pm 0.04	1.00 \pm 0.05
Organic Horizon Mass (Mg/ha)	81.8 \pm 35	82.4 \pm 66	60.1 \pm 40
Organic Horizon Mass (Mg/ha) [*]	188 \pm 36	378 \pm 51	139 \pm 25
Carbon Concentration (Mg/ha)			
Organic	17.6 \pm 6.3	19.4 \pm 11.7	14.0 \pm 12.8
Mineral	31.9 \pm 9.8 ^a	16.8 \pm 5.1 ^b	23.6 \pm 5.5 ^{bc}
Nitrogen Concentration (Mg/ha)			
Organic	0.62 \pm 0.23	0.89 \pm 0.56	0.42 \pm 0.36
Mineral	1.34 \pm 0.49 ^a	0.75 \pm 0.40 ^b	0.87 \pm 0.17 ^{bc}
C:N Ratio			
Organic	28.41 \pm 4.8	23.94 \pm 4.9	29.10 \pm 13.1
Mineral	24.21 \pm 4.0	23.69 \pm 5.4	25.56 \pm 2.4
Top 10 cm [*]	22.8 \pm 1.95	25.2 \pm 1.32	29.5 \pm 2.15

Notes: small letters represent significance between treatments according to Tukey's HSD test ($p < 0.05$). ^{*} Data from Rumbaitis del-Rio, taken in 2001 and 2002.

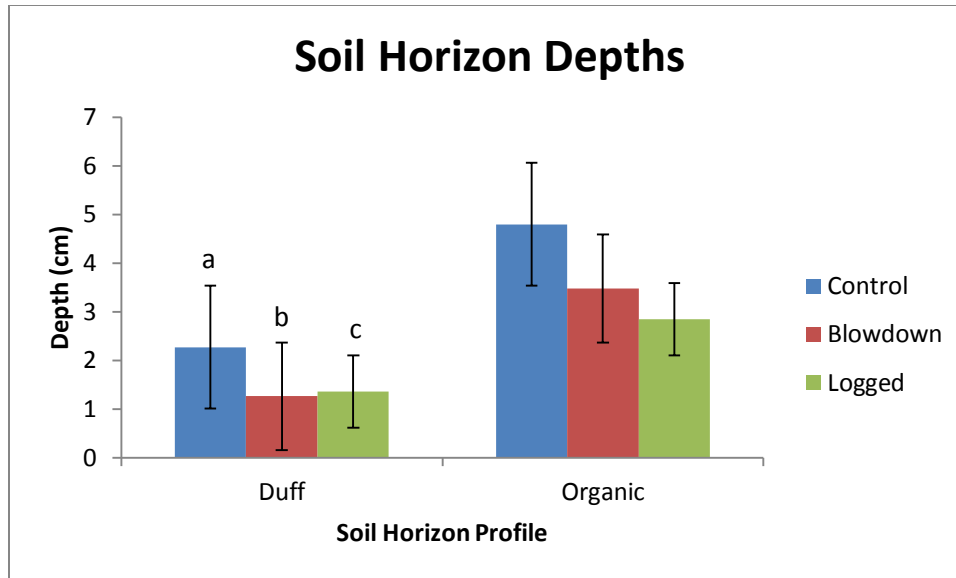


Figure 2: Average depths of duff, organic, and mineral soil horizons in centimeters. Soil horizon depths were measured directly in the field. N=10 plots per treatment. (Note: letters represent significant differences- refer to Table 1) Bars represent standard error.

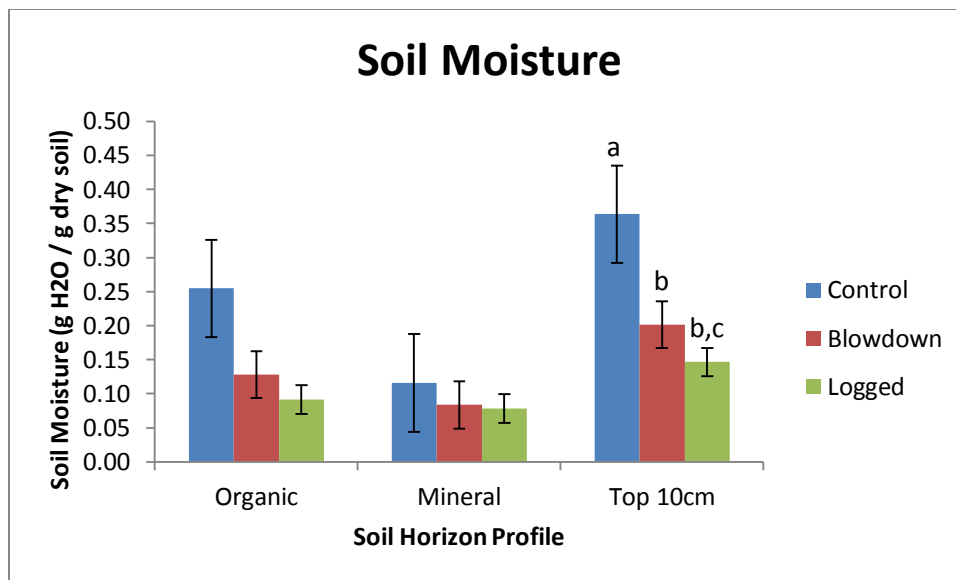


Figure 3: Average soil moisture (grams of water per grams of dried soil) values associated with the organic and mineral soil horizons and top 10 cm of soil across treatments. Soil moisture of the top 10cm was significantly different between treatments. N=10 plots per treatment. (Note: letters represent significant differences- refer to Table 1) Bars represent standard error.

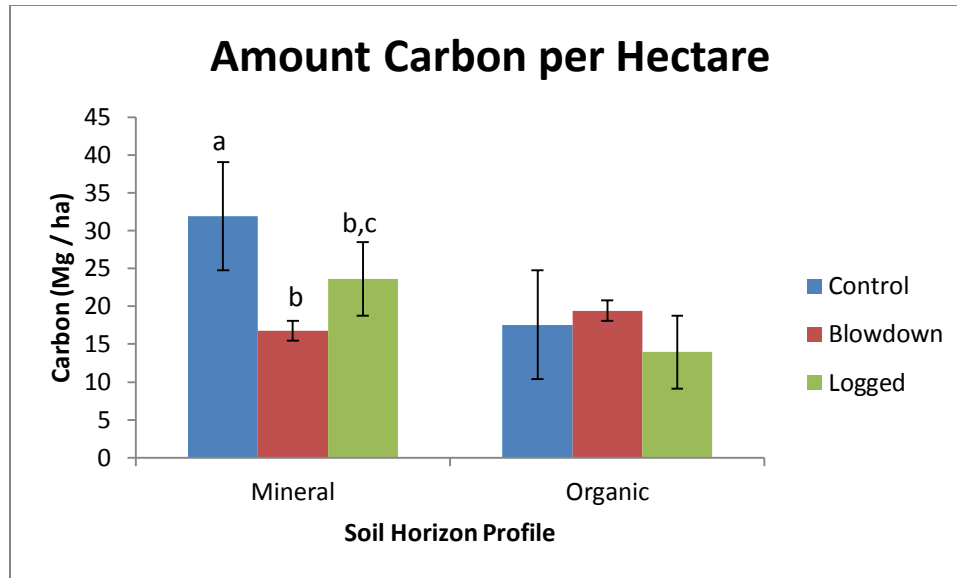


Figure 4: Average amount of carbon (in mega-grams per hectare) compared across treatments for the organic and mineral horizons. Mineral horizons showed significant treatment difference (Note: letters represent significant differences- refer to Table 1) Bars represent standard error.

Regeneration Characteristics

Seedling density per hectare did not show significance (Table 2; Fig. 5, $F(11, 18) = 2.032$, $p = 0.09$) caused by a significant effect of aspect ($p = 0.03$), and treatment ($p = 0.04$). After controlling for the effects of topography, the significant treatment effect was determined to be caused from a marginally significant difference between control and blowdown treatments ($p = 0.053$). Fir density per hectare (Table 3; Fig. 8) showed significance ($F(11, 18) = 2.87$, $p = 0.023$) with a significant effect from aspect ($p = 0.003$) and an interaction between aspect and logged treatment ($p = 0.004$). After controlling for these effects, there was a significant treatment effect ($p = 0.01$) and an interaction between treatment and aspect ($p = 0.02$). Tukey's HSD revealed the significant treatment effect to be caused by a significant difference between control and blowdown treatments ($p = 0.014$). Spruce density per hectare similarly showed significance ($F(11, 18) = 5.986$, $p = 0.0005$), caused by a highly significant effect from slope ($p = 0.0005$), and aspect

($p = 0.003$), and significant interactions between slope and control treatment ($p = 0.043$) and logged treatment ($p = 0.0008$) and between aspect and control treatment ($p = 0.025$) and logged treatment ($p = 0.004$). Further analysis showed a significant effect of elevation ($p = 0.0004$), treatment ($p = 0.006$), and an interaction between slope and treatment ($p = 0.006$) and between aspect and treatment ($p = 0.011$). Tukey's HSD revealed the significant treatment effect to be caused by a significant difference between control and blowdown treatments ($p = 0.004$) and between logged and control treatments ($p = 0.061$). Lodgepole density per hectare (Table 2; Fig. 8) after controlling for the effects of elevation, slope and aspect and any interactions between treatment and elevation, slope or aspect showed no significant treatment differences ($F(11, 18) = 0.648, p = 0.767$). Aspen density per hectare (Table 2; Fig. 8) after controlling for the effects of topography showed no significant treatment differences ($F(11, 18) = 0.6512, p = 0.764$).

Ground Cover Properties

The total coarse woody debris (Mg/ha) after controlling for the effects of elevation, slope, and aspect, and the interactions between treatment and elevation, slope or aspect showed a significance ($F(11,18) = 4.257, p = 0.003$, Fig. 6), caused from a significant effect of treatment ($p = 0.0003$), and an interaction between slope and treatment ($p = 0.016$). After these effects of the interaction between slope and treatment were removed, the treatment effect was determined to be caused by a significant difference between control and blowdown treatments ($p = 0.0006$), and blowdown and logged treatments ($p = 0.028$).

Fractional cover (Table 2, Fig. 7) was separated into functional groups of most importance, forbs, graminoids, rocks, bare, coarse woody debris, and litter. Fractional cover of rocks ($F(11,18) = 0.8732, p = 0.5795$), coarse woody debris ($F(11,18) = 1.09, p = 0.4203$), bare soil, ($F(11,18) = 0.5626, p = 0.8342$), and litter, ($F(11,18) = 0.503, p = 0.877$) after controlling for

the effects of elevation, slope, aspect and the interactions between treatment and elevation, slope or aspect showed no significant treatment effects. Fractional cover of forbs did show a significant relationship after controlling for elevation, slope, aspect and their interactions with treatment ($F(11,18)= 3.672, p= 0.007$). Further analysis determined this relationship to be caused by treatment ($p= 0.0006$) and aspect ($p= 0.0447$). The treatment effect was determined to be caused by a significant difference between control and blowdown treatments ($p= 0.002$), and between logged and control treatments ($p= 0.005$). Fractional cover of graminoids also showed a significant relationship after controlling for the effects of elevation, slope, aspect and their interactions with treatment ($F(11,18)= 3.605, p= 0.008$). Further analysis determined the relationship to be caused by elevation ($p=0.0398$) and treatment effects ($p= 0.0009$), which was caused by a significant difference between control and blowdown ($p= 0.0136$), and between logged and control treatments ($p= 0.006$).

Table 2:

Averages and standard deviation of the regeneration and understory characteristics across treatments. (\pm S.D.) N=30, 10 plots per treatment.

Treatment	Control	Blowdown	Logged
Seedling Density per ha	3875.5 \pm 3112.2	2395.56 \pm 1501.5	2026.67 \pm 787.5
Total CWD (Mg/ha)	37.701 \pm 16.31 ^{ac}	98.909 \pm 46.90 ^b	52.684 \pm 21.42 ^c
Woody Debris (Mg/ha)*	42 \pm 13	399 \pm 58	139 \pm 25
Fractional Coverage- Forbs	36.556 \pm 20.21 ^a	18.460 \pm 6.93 ^b	12.410 \pm 5.27 ^c
Fractional Coverage- Gramm.	10.767 \pm 13.71 ^a	23.710 \pm 8.66 ^b	33.130 \pm 7.45 ^c

Notes: small letters represent the significance between treatments ($p<0.05$). *Data from Rumbaitis del-Rio, taken in 2001 and 2002.

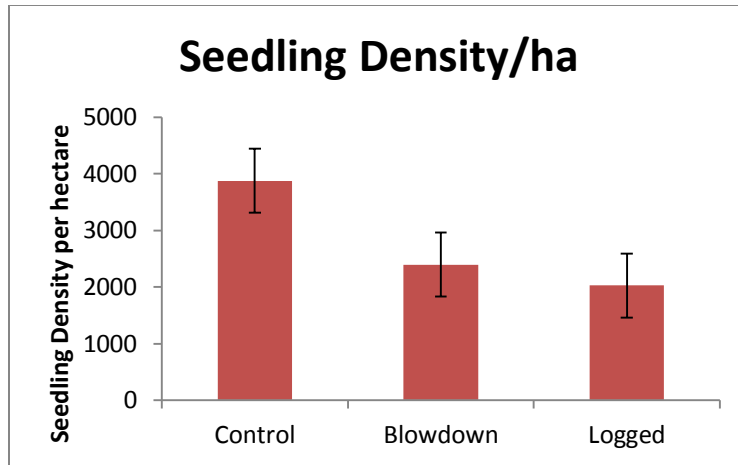


Figure 5: Seedling densities per hectare across treatments. N=30, 10 plots per treatment. (Note: letters represent significant differences between treatments ($p = <0.05$), error bars show standard error)

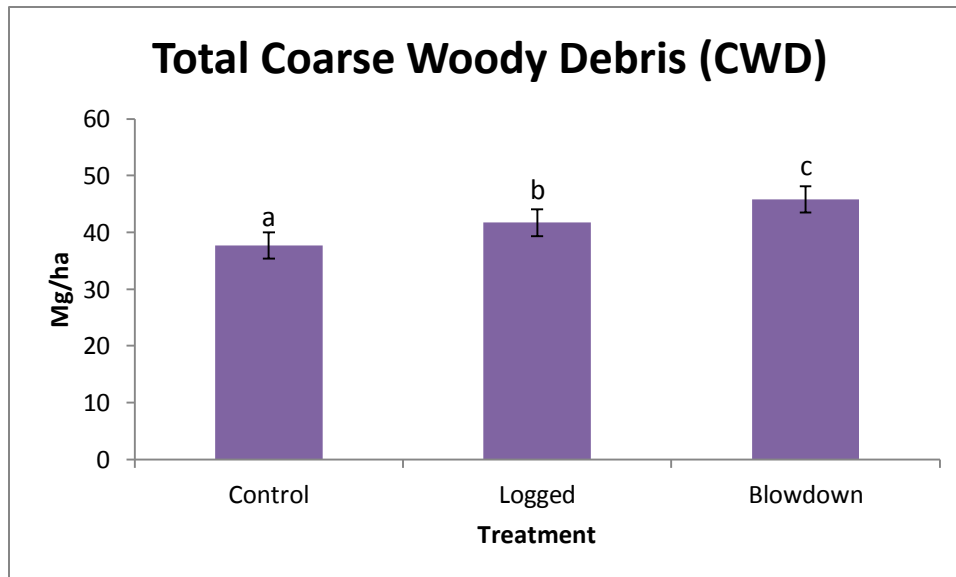


Figure 6: Total amount of coarse woody debris (Mg/ha) across treatments. N=30, 10 plots per treatment. (Note: letters represent significant differences between treatments ($p = <0.05$), error bars show standard error)

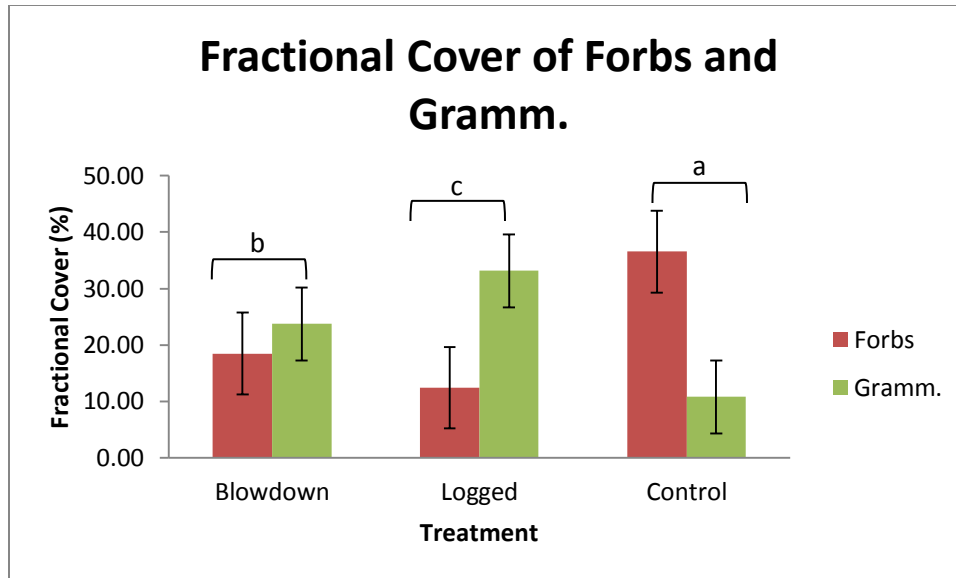


Figure 7: Fractional cover of forb and graminoid species across treatments, which were determined to be the only fractional coverage functional groups showing a statistical significant effect from treatment. (Note: small letters represent significant differences between treatments ($p = <0.05$), error bars show standard error)

Table 3:

Number of seedlings per species across treatments. Note: small letters (a,b,c) show significance across treatments for differences in number of species. N=30, 10 plots per treatment.

Treatment	Fir	Spruce	Lodgepole	Aspen
Control	712 ^a	115 ^a	1	32
Blowdown	368 ^b	29 ^b	23	100
Logged	182	27 ^{bc}	135	98

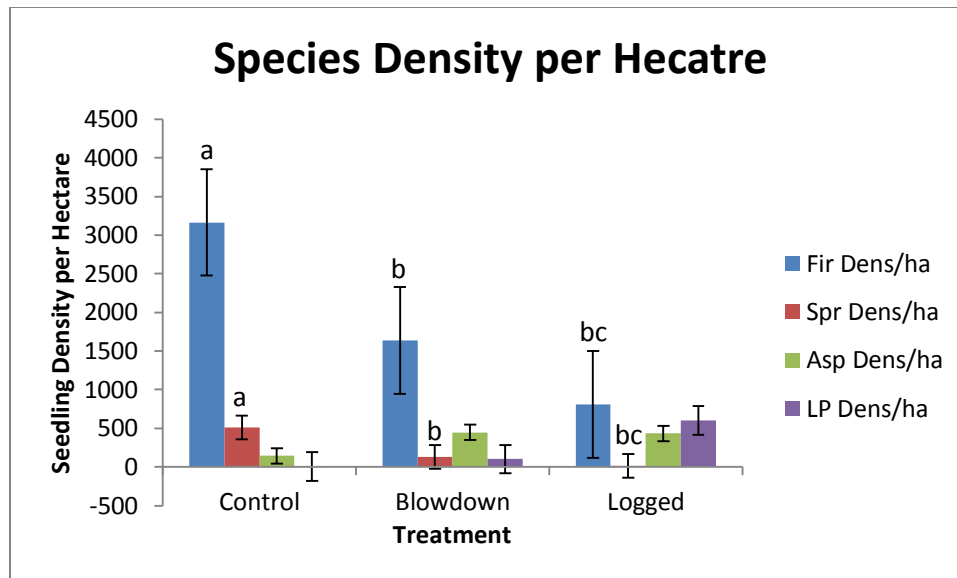


Figure 8: Average seedling density by species across treatments. N=30, 10 plots per treatment. (Note: letters represent significant differences between treatments ($p = <0.05$), error bars show standard error)

Discussion

Disturbances are widely acknowledged to be an important part in ecosystem structure and functioning; yet, little is known about the effects of multiple compounding disturbance effects on soil and subalpine forest regeneration (Rumabitis-del Rio 2006, Buma and Wessman 2011, Kulakowski et al. 2013). There is growing interest in evaluating the effects of management activities following natural disturbances on the ecosystem's ability to recover and its corresponding community composition, especially concerning the effects of salvage-logging (Dellasala et al. 2006). The present study represents one of few studies evaluating the long-term effects from blowdown and subsequent salvage-logging in a subalpine forest, with the benefit of being able to compare assessments made immediately after the disturbance (Rumbaitis del-Rio 2006) and via the present study 10-15 years post-disturbance.

The present study assessed the following questions: 1) What are the long-term effects of multiple disturbances and their interactions on species composition and forest structure in a

subalpine ecosystem? 2) Will the differences in soil properties initially observed between treatments remain 15 years after the events? 3) Does regeneration remain lower in logged blowdown areas 15 years post disturbance? 4) Are there changes to species composition in logged blowdown areas?

The results of this study suggest some long-term effects from the compounding disturbances of blowdown and salvage-logging on subalpine forest recovery, while the magnitude of changes in soil characteristics seen immediately following the disturbances was generally diminished 10-15 years post disturbance. Significant difference between treatments for nearly all soil characteristics were found to be reduced over time. The depth of duff supported previous research and was deepest in control plots and lowest in blowdown plots, which is likely correlated with the loss of canopy trees from the blowdown plots (Cooper-Ellis et al. 1999), which in turn reduced the amount of litter and subsequently duff (Baker et al. 2002). The depth of the organic horizon was initially observed to be significantly different between treatments, but this study found no significant treatment differences. The depth of the organic horizon in the logged treatment was higher than initially observed, suggesting that over time the soil horizon profiles have begun to homogenize to be more like pre-disturbance characteristics (Everham and Brokaw 1996). This change over time is supported by previous studies in deciduous forests of comparable time scales (Allen et al. 2012). Although the ecosystem dynamics are different between deciduous and coniferous forests, it is interesting to view this similarity.

The soil moisture of the top 10 cm of soil was significantly different between control and both blowdown and logged plots, and followed the same trend as duff (Table 1). This is supported by previous studies (D'Amato et al. 2008; Peterson and Leach 2008b) that found significant reductions in soil moisture following salvage-logging. The effects of salvage-logging

following disturbance have been seen to increase the surface temperature (Greene et al. 2006), which in turn reduces soil moisture (Beschta 1995) as was also found in the present study's findings of lower soil moisture in the logged blowdown patches. Unexpectedly, the present study's findings for soil horizon depths, contradict initial observations from 2000-2002 (Rumbaitis del-Rio 2004), in which no significant differences in soil horizon depths between treatments were recorded. The differences between the initial and present analyses with respect to soil horizon depths is consistent with previous studies conducted in subalpine *Picea-Abies* forests (Scott-Denton et al. 2003) suggesting that the depth of the organic soil horizon varies spatially. This variation may be representative of the differences in site microclimate, which at the time of initial observations presumably had different levels of soil compaction, horizon depth, and regeneration.

Similarly, unlike previous studies evaluating the effects of salvage-logging following disturbance (Beschta 1995), none of the present study's bulk density measurements were significantly different between treatments. This discrepancy may be a function of the length of time after the disturbance to when observations were recorded (Hart and Sollins 1998), or due to differences in disturbance severity (Kulakowski et al. 2003). The trends for bulk density found here, albeit not significant, suggest that soil compaction is higher in logged blowdown sites, which is consistent with significant trends initially observed (2000-2002). This change from significance to non-significance is consistent with previous work conducted in boreal forests (Hood et al. 2003) over a comparable time scale, suggesting that soil compaction resulting from salvage-logging diminishes over time.

Not surprisingly, there was a difference in carbon and nitrogen concentrations between organic and mineral soil horizons. There was a significant difference between logged and control

treatments for both the concentration of carbon and nitrogen (Table 1) within the mineral horizon. Previous studies (Hood et al. 2003) suggest that soil carbon and nitrogen decrease with increasing elevation, which may explain these results (due to the differences in treatment plot locations). Others also found that soil nitrogen decreases following disturbance which supports the results obtained in the present study (Olsson et al. 1996). The C:N ratios support the trends initially observed in 2000-2002, although the significant treatment differences were no longer evident. This corroborates previous studies (Johnson and Curtis 2001, Kramer et al. 2004), which suggest that salvage-logging produces an initial increase in soil carbon and nitrogen.

Similar to what previous studies suggest (Kulakowski et al. 2003), the seedling density was found not to be significantly different between treatments. However, the relative species density for fir and spruce were significantly different between treatments. Both fir and spruce density were highest in control plots. This contradicts a report within the same blowdown area that there were more fir and spruce in blowdown plots than in undisturbed plots (Kulakowski and Veblen (2003). This dissimilarity in findings may be accounted for by the increase in surface temperature in disturbed plots, which may increase seedling mortality (Veblen et al. 2001, Elliott et al. 2002, Greene et al. 2006). Also, given that more than a decade has passed, seedling establishment is likely to have declined over time. Moreover, unlike what some recent studies (Kulakowski et al. 2013) have predicted, there was not a significant difference in aspen seedling density between treatments. This could be a result of pre-disturbance stand characteristics, which have been found to be important in determining blowdown severity (Veblen 2003) and regeneration (Baker et al. 2002).

The total coarse woody debris, as expected and supported by previous studies (Rumbaitis-del Rio 2006, D'Amato et al. 2011), was highest in blowdown plots and significantly

different from control and logged blowdown plots. Although, there was much less total coarse woody debris present than what had been recorded in 2001-2002, the same trends are present in this study, and will likely remain for many years (Tinker and Knight 2000, Kulakowski and Veblen 2003, Peterson and Leach 2008a).

The fractional ground cover of forb and graminoid functional groups was significantly different between treatments, similar to what Rumbaitis-del Rio (2006) reported. The amount of graminoid cover was lowest in control plots, similar to previous research (Rumbaitis-del Rio 2006) which suggests the canopy reduces light availability to understory species in healthy-mature subalpine *Picea-Abies* forests (Ulanova 2000, Greene et al. 2006, Lang et al. 2009). Ground cover of forbs was higher in blowdown than in logged blowdown plots, also supported by previous studies (Greene et al. 2006, Rumbaitis-del Rio 2006), which suggests that blowdown events that create tip-up and mound soil disturbances allow for rapid establishment of herbaceous understory species from the increased light and nutrient availability (Everham and Brokaw 1996, Cooper-Ellis et al. 1999, Rumbaitis-del Rio 2006).

Limitations

The variability of topography within and between treatments significantly affected nearly all statistical tests conducted in this study, and likely reduced treatment effects. Although the effects of topography were controlled for through the use of analysis of covariance, there would likely have been more detectable treatment effects if the study plots had been located on sites with more similar elevations, slopes and aspects. However, given the spatial distribution of the disturbances and the high topographical variability characteristic of subalpine environments, this site in particular, this can only be controlled for through sample size. The sample size per treatment (ten plots per treatment), was relatively large for the amount of measurements per plot,

however during statistical testing the sample size appeared to reduce the degrees of freedom and potentially significant treatment differences as a function of having to remove the effects of topography.

Conclusions

The results of this study confirm the primary hypothesis, in which salvage-logged blowdown plots showed reduced regeneration and differences in soil characteristics compared to intact and blowdown plots 10-15 years post disturbance. Although many of the significant differences between treatments initially observed post-disturbance had diminished 10-15 years later, the trends in lower seedling density, reduced carbon and nitrogen concentrations and higher soil compaction were still observed in salvage-logged plots. Salvage-logged plots were found to be much less similar to control plots than blowdown plots. This was particularly evident in the percent cover of grasses within the salvage-logged plots which was significantly higher compared to control or blowdown plots. This suggests that as succession continues, blowdown plots will reestablish pre-disturbance characteristics to resemble control plots more closely than will salvage-logged plots. The consequences of this may result in the salvage-logged blowdown plots more closely resembling subalpine meadows as time progresses.

It should be recommended that salvage-logging not be performed following severe disturbance events in order to minimize the detrimental effects on forest recovery and regeneration. Future research may be able to provide insights of even longer term responses of forest regeneration following compound disturbances to better understand the time required for the stabilization of forest recovery in subalpine ecosystems. This may include evaluating the potential implications of having an ecosystem regime shift away from spruce-fir forest to having

subalpine meadow. There also needs to be a better understanding of the influences of topographic gradients when evaluating subalpine forest response to salvage-logging following blowdown disturbances.

With the increasing threat of climate change, understanding of compound disturbances needs to be incorporated into future research and land management decisions. The unpredictability associated with changes in climate may result in more frequent or more severe disturbances. Therefore there is a need for management agencies to better evaluate the effects of their decisions on the recovery and resilience of disturbed ecosystems. Interacting or compounding effects of multiple disturbances can be observed and thus successional processes occurring on long-term scales need to be incorporated into future disturbance research.

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